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# THE GENETIC BEHAVIOR OF MICE OF THE COLOR VARIETIES "BLACK-AND-TAN" AND "RED"

L. C. DUNN

Bussey Institution

Early in 1914 there were received at the Bussey Institution certain stocks of mice obtained from fanciers in England. Some preliminary studies of the mice were made by Professor Castle and Dr. Little. A more intensive study of one race, the black-eyed-white, was afterward made by Dr. Little and independently by Dr. Detlefsen. The remaining stocks were turned over to Mr. W. F. Whittier, who carried on experiments with them partly at the Bussey Institution, partly at the Massachusetts Agricultural College, recording some 2,500 offspring. After devising the color grading scale and the general methods followed in the later experiments, he relinquished the work to the present writer. Since that time about 2,000 young have been recorded, bringing the total to 4,500. All the work has been done under the advice and direction of Professor Castle.

The principal varieties which have been used in these experiments are known in England as "black-and-tans" and "reds." The genetic character of these mice was at the outset quite unknown, and in this paper it is proposed to give some account of their genetic behavior, and since they have proved to be forms of yellow mice, to assign to them and their derivatives places in a scheme of classification of the yellow varieties.

The black-and-tan race has presented throughout the more interesting problem. In appearance these mice are of an intense shiny black dorsally, with a belly superficially clear yellow. The belly hairs, however, are marked by having dull black bases, hidden by the longer and overlying yellow areas of the hairs. Yellow-ticked hairs are occasionally seen on flanks and head, encroaching on the black pigmented parts. This peculiarity increases somewhat with age, but never to such an extent as to make the body color predominantly yellow.

When bred *inter se,* they have been found invariably to be heterozygous, no homozygous black-and-tan having been discovered among a dozen individuals tested by suitable matings. As recessives they have given all-black mice more intense than any we have seen derived from other sources. Forty-two matings *inter se* of pure-bred black-and-tan parents produced 148 young, an average of 3.52 to a litter. Of these young 93 have been black-and-tan and 55 black, a ratio of 1.69 : 1. This approximates a 2 : 1 ratio more closely than the 3 : 1 ratio usually given by Mendelian heterozygotes. The black recessives breed true, and when mated to black-and-tans have produced equal numbers of black-and-tan and black young (18 : 18). The approximation of a 2 : 1 ratio in matings of black-and-tans *inter se* shows their gametic similarity to yellow mice whose unfixable nature was first shown by Cuénot ('03). Figures given by this author combined with those given by Castle and Little ('10), by Little ('10 and '11) and by Miss Durham ('11) total 2,673 young produced by yellow × yellow matings. Of these 1,783 were yellow and 890 non-yellow, a ratio of almost exactly 2 : 1.

The small average size of litters produced by black-and-tan parents mated *inter se* gives added evidence of their resemblance to yellow. Castle and Little ('10), in confirmation of Cuénot's observations, showed that yellow × yellow matings produced litters of smaller average size (4.71) than yellow × non-yellow (5.57), and following Cuénot they attributed the difference to absence of homozygous, yellow-yellow zygotes. The 2 : 1 ratio and the small-sized litters serve also to relate the black-and-tans with Castle's "sooties" and Miss Durham's "sables," both of which were shown to be heterozygous yellows carrying black as a recessive.

The reds, by their appearance, gave promise of being some form of yellow. The color, as the name implies, is orange-red dorsally, the belly being a lighter shade. Up to the age of three weeks the young mice are dusky yellow-red, the red apparently being obscured by a darker pigment. As they grow older they become progressively of a brighter and more intense reddish hue.

Genetically these mice behave much like black-and-tans. None has been found which has bred true, and the relation of reds to non-red recessives is in the same approximate ratio of 2:1. The recessives in this case are "chocolate," in color a deep, rich brown, showing an intensity comparable to that of the blacks derived from the black-and-tans. Thirty-one matings of red with red have produced a total of 136 young, of which 77 have been red, and 59 brown, a ratio of 1.30:1. The average size of these litters was 4.40. Eleven matings of red with brown produced 34 red and 31 brown young (equality expected), the average size of litters here being 5.90.

So far we have dealt only with the pure stocks, each of which is fairly uniform, although small fluctuations in density of pigmentation do occur. When, however, these two sorts are crossed with each other, yellow mice of various shades are obtained, which form two graded series, roughly parallel, one bearing black pigment and producing black recessives; the other bearing brown pigment and producing brown recessives. Classification in these two series is complicated by the fact that juvenile colors are not uniformly retained, but in some cases increase and in other cases decrease in intensity when the fur is moulted. All animals have therefore been assigned a numerical color-grade at the age of three weeks, this age having been determined as the time when the relation of yellow to black or brown pigment is most definitely visible; and although many animals have been re-graded at intervals throughout life, each has been designated by his original grade.

The cross of black-and-tan with red produced in $F_1$ two classes of young. (1) One of these may be described as a black-and-tan in which the black pigmentation is lessened in amount and intensity, this decrease being attended by an increased development of yellow pigmentation. This class closely resembles the variety known as sable. (2) The other class of young consisted of blacks, which also were less intensely pigmented than the recessives produced by pure-bred black-and-tans mated *inter se.* It was found convenient in classifying the young of later generations to recognize six arbitrary grades of blackness of which yellow (showing no black pigment) forms grade 1, and black-and-tan grade 6. On this scale the mean of the $F_1$ "sable" young was close to 3.5, the intermediate point between yellow and black-and-tan. The distribution can be plotted by translating the descriptive terms in Mr. Whittier's notes into terms of numerical grades, as follows:

| | | | | |
|---|---|---|---|---|
| Grade | 3, | 4, | 5, | 6 |
| Frequency | 9, | 0, | 6, | 1 |

These descriptive notes were made before the grading scale had been adopted, and it is quite probable that no real discontinuity in the variation occurred as would be suggested by entire absence of animals of grade 4. No such discontinuity is found in the work done since the grading scale was adopted.

The $F_1$ black young were mated *inter se* and back-crossed with browns to test their gametic composition. When mated *inter se* they gave 28 black and 11 brown young, nearly a 3:1 ratio (29:10). Back-crossed with browns they gave 37 blacks and 33 brown young, nearly a 1:1 ratio (35:35). $F_1$ blacks apparently, then, were simple heterozygotes, not differing from ordinary heterozygotes produced by crossing homozygous black with homozygous brown.

Thirteen of the $F_1$ sables were tested by mating with browns. One hundred and thirty-three young resulted, of which 70 were yellows of various shades and 63 non-yellows. Of this latter group 32 were black and 21 were brown, equality being expected. The yellows also may be divided into two groups, in one of which the eyes and fur contain black pigment, while in the other the corresponding parts contain brown pigment. In both of these yellow groups the amount of black or brown pigment varied. Again translating Mr. Whittier's descriptions into terms of the numerical scale, we have the following distribution:

| Grade... | 1, | 2, | 3, | 4, | 5, | 6, | Total |
|---|---|---|---|---|---|---|---|
| (1) The black series—Frequency... | 0, | 4, | 8, | 3, | 8, | 2 (?), | 25 |
| (2) The brown series—Frequency.. | 13, | 1, | 4, | 16, | 1, | 2, | 37 |

It was frequently found to be impossible to determine by inspection alone whether a particular yellow animal belonged to the black or the brown series, because yellow fur containing a small amount of black pigment closely resembles that which contains a considerable amount of brown pigment. Consequently these back-cross young (produced by an F$_1$ sable mated with brown) had to be tested themselves, either by *inter se* matings or by crossing with browns. The classification of the back-cross young in the above tables is based partially on breeding tests and in the cases where these were lacking classification is based on inspection at the age of three weeks. It is uncertain whether any individuals were obtained from the F$_1$ sable × brown cross which showed the full intensity of pure-bred black-and-tans (grade 6), although two animals are recorded in the notes as black-and-tan without qualifying terms.

As a result of back-crossing with browns the F$_1$ sables (out of black-and-tan × red) and testing the young produced by crossing them with browns, two graded series of yellow mice may be recognized as follows.

| Black Series | | | Brown Series | | |
|---|---|---|---|---|---|
| Grade | Designation | Producing as Recessives | Grade | Designation | Producing as Recessives |
| 6 | Black-and-tan | Black | 6 | Brown-and-tan | Brown |
| 3–5 | Black-sable | Black | 3–5 | Brown-sable | Brown |
| 2 | Sooty yellow | Black | 2 | Red | Brown |
| 1 | Yellow | Black | 1 | Yellow | Brown |

The brown-and-tan and brown-sable varieties are new. They resemble black-and-tan and black-sables, respectively, in which all black pigment in the fur has been replaced by brown pigment. The parallelism between the two series is strongest at top and bottom; red has no exact counterpart in the black series, since its yellow is more intense than that of sable. All members of the two series when crossed *inter se* fluctuate about their parental mean grade. The greatest fluctuations are noted among the offspring of sables; the least among black-and-tans and reds. We suspect also that a like gradation occurs in the amount and intensity of black and brown pigments in the black and the brown recessives of these series, though on account of the self color of these varieties this point is difficult of verification, except by breeding tests. From some tests which have been made and others which are under way, the evidence seems to show that blacks from sables and yellows have less intense young when crossed with agoutis, than do the blacks out of pure black-and-tan. Tables and curves for this cross will be given at a later time.

It is significant now that sables and black-and-tans may be synthesized by a cross of blacks out of the black-and-tan race with reds, showing that the black recessives carry the same differentiating element as do the black-and-tans. Such a cross produced 45 young, 20 of which were black-and-tan or sable, while 25 were black. The $F_1$ blacks were heterozygous for brown, *inter se* matings producing 32 blacks and 13 browns.

When a black which was heterozygous for brown was mated to a red, yellows falling in both the black and the brown series were produced as follows:

*Black Series*

| Grade | 1, | 2, | 3, | 4, | 5, | Blk., | Total |
|---|---|---|---|---|---|---|---|
| Frequency | 1, | 1, | 2, | 0, | 2, | 1, | 7 |

*Brown Series*

| Grade | 1, | 2, | 3, | 4, | 5, | Br., | Total |
|---|---|---|---|---|---|---|---|
| Frequency | 1, | 2, | 0, | 3, | 1, | 6, | 13 |

The element added in this last cross is plainly the brown gamete carried by the black. This brown gamete, however, has received something additional from the black-and-tan race, so that when red unites with this changed brown gamete the result is a darkening and intensification of the brown pigments to produce a brown-and-tan or brown-sable, a process quite parallel to that which produces black-and-tan and black-sable in the pure black × red cross.

A few crosses were made between pure-bred black-and-tan and brown, and although the numbers here are small, the indication is that the result will be the same as in the black × red cross. $F_1$ consisted of blacks and black-sables; the sables when back-crossed to browns gave approximately equal numbers of blacks (26) and browns (20) and also the two yellow series as follows:

| | | | |
|---|---|---|---|
| Black sables (mean grade 3.5) | 11 | Brown sables (mean grade 4) | 10 |
| Yellows and sooties | 3 | Reds and yellows | 10 |
| Total | 14 | Total | 20 |

This back-cross with the recessive brown gives a direct index of the yellow gametes of the $F_1$ sables. That they vary in darkness should be borne in mind during the discussion of the difference between black-and-tan and yellow.

The reds in suitable crosses showed the same tendency to produce fluctuating blends. Mated with creams they gave yellows of an intermediate shade (16) and recessive non-yellows (10). These light reds were bred *inter se* and tested by crossing with browns. The young (100 in number) fluctuated in intensity about the shade of the light red parent or parents. Full intensity was not recovered except in back-crosses. Hence red is likewise a form of yellow, differing from it by an added intensity which blends in crosses.

The foregoing evidence has merely pointed to the yellow nature of black-and-tan and red; has classified them and their derivatives among the yellows, and has hinted at the possible difference between these forms and ordinary yellows. It is time now to inquire as to the real genetic nature of these mice, and to attempt a preliminary explanation of their differences from yellow. By far the largest number of mice have been bred and are being bred toward this end.

Let us consider first the black-and-tan variation. By its behavior it evidently forms two sorts of gametes, black-and-tan (yellow) and black. Each of these has an added something which makes the zygote into whose composition it enters darker than ordinary yellow or black. We may call this something "darkener"—be it singular or plural—and indicate the gametes by YD and BD. Red, similarly, forms gametes red (yellow) and brown; and these also show an addition which we may call "intensifier." The gametes of red are then YI and bI. The sables produced by red × black-and-tan can only be referable to a union of YD and bI, or YI and BD since YDYI is non-viable, and since YDbI and YIBD unions have been demonstrated in the brown × black-and-tan and red × black crosses, respectively, and have produced in both of these latter cases similar sables. The presence of the darkener and the intensifier in the same zygote weakens both and demonstrates their physiological and genetic independence.

The next point to be noted is that both darkener and intensifier are variable. All gametes formed by zygotes containing D or I are not equivalent in their D or I content. It is possible to demonstrate this for the darkener; the variable intensification from crosses with red cannot yet be as satisfactorily shown on account of the difficulties of grading. For light on the action of the darkener we may turn to the agouti crosses.

The ordinary wild house-mouse when bred pure, shows the agouti pattern and gray color with great uniformity. It possesses the black and yellow pigments of the black-and-tan mouse as well as brown pigment, but contains no factor to dilute or darken these pigments. These facts make it an ideal race with which to test for a suspected darkener which acts on the black pigment of a yellow mouse.

Yellow, Cuénot showed, is an allelomorph of agouti and non-agouti. Black-and-tan, in turn, is not an alternative form of agouti like the light-bellied gray mouse, but a yellow, and hence should be allelomorphic to agouti. And such it is as far as its yellow component is concerned, but not as regards its darkener. The $F_1$ young from a cross of black-and-tan by wild agouti vary in darkness about a mode midway between black-and-tan and agouti. Black-and-tan we may regard as full darkness and assign to it an arbitrary grade of 6. Wild agouti we may regard as entire absence of this darkness and assign to it the grade 1. $F_1$ from a cross of these two has consisted of two sorts of young. (1) The first sort may be considered as the result of a union of the YD gamete from black-and-tan with the agouti gamete. These mice have been called sable agoutis; since they have the general pattern of sables. The bellies are yellow; the darkness of the dorsal hairs is variable through the same range as that of the sables, while all hairs on flanks, head and parts of the back are agouti ticked. These yellow $F_1$ young graded on the sable scale show the following distribution:

| Grade | 2, | 3, | 4, | 5, | Total |
|---|---|---|---|---|---|
| Frequency | 1, | 15, | 7, | 4, | 27 |

(2) The second sort of $F_1$ young may be called non-yellow and referred to a union of the BD gamete from black-and-tan with the agouti gamete. These are simply much-darkened agoutis. The belly is gray like the wild agouti and the flanks are agouti ticked. The head and middle of the back are covered by hairs which are black for most of their length, a very narrow yellow band being present near the tip, or in some cases lacking entirely in an area of hairs down the center of the back. This type is known as dark agouti and has also been graded according to darkness on a scale parallel but not exactly equiva-

lent with the sable scale. Grade 1 was taken as ordinary wild agouti; grade 6 was taken as a gray-bellied black in which the agouti pattern had been lost and in which the darkness was equivalent roughly to that of the black-and-tan. In grade 2 the extent of black in each hair is increased, and the wide yellow band diminished; in grade 3 the yellow is left only in a narrow band; in grade 4 the yellow ticking is lost from hairs in a streak down the center of the back and in grade 5 the area of all black hairs is extended to cover the whole back, ticking being limited to the sides of the body. On the basis of such a scale the $F_1$ dark agoutis were distributed as follows:

| Grade | 2, | 3, | 4, | Total |
|---|---|---|---|---|
| Frequency | 8, | 23, | 5, | 36 |

These $F_1$ dark agoutis bred *inter se* have produced 155 young, of which 109 have been dark agouti and 46 black, indicating that the $F_1$ dark agoutis were heterozygous for black. The distribution of 58 of these $F_2$ dark agoutis is as follows:

| Grade | 1, | 2, | 3, | 4, | 5, | Total | Mean Grade |
|---|---|---|---|---|---|---|---|
| Frequency | 17, | 21, | 11, | 7, | 2, | 58 | 2.2 |

By using as parents the darkest of these agoutis, regardless of generation, dark agoutis were obtained, which when three weeks old approximated the grade 6. They resemble all-black mice with gray bellies except for occasional ticked hairs on their flanks.

It will be remembered that all darkness in these dark agoutis was acquired originally from the BD gamete of a black-and-tan mouse, since the range of darkness in the wild agouti used has never been above grade 1. Careful grading of the young from matings among dark agoutis should then furnish information as to the variation in the "darkener." If the "darkener" is a multiple thing such matings should afford it opportunity to segregate or Mendelize. A tabulation of matings among all classes of dark agoutis of the young born since the introduction of the grading scale follows:

DISTRIBUTION BY GRADE OF YOUNG PRODUCED BY DARK AGOUTI PARENTS OF VARIOUS GRADES

| Parents | Grade Distribution of Young | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 5.5 | 6 | Total Agouti | Mean Grade | Black Young |
| 1 × 1 | 32 | | | | | | | 32 | 1.00 | 1 |
| 2 × 2 | 11 | 21 | | | | | | 32 | 1.65 | 1 |
| 4 × 2 | 10 | 17 | 5 | 2 | | | | 34 | 2.00 | 1 |
| 4 × 3 | | | 6 | 5 | | | | 11 | 3.45 | 1 |
| 4 × 4 | | | 6 | 7 | | | | 13 | 3.46 | 0 |
| 5 × 4 | | 1 | 11 | 8 | 18 | 4 | 4 | 46 | 4.41 | 14 |
| 5 × 5 | | 1 | 11 | 15 | 11 | 9 | 4 | 51 | 4.34 | 8 |
| 6 × 4 | | 1 | 4 | 15 | 13 | 4 | 9 | 46 | 4.28 | 2 |
| 6 × 5 | | | 4 | 11 | 11 | 18 | 7 | 51 | 4.94 | 12 |
| 6 × 6 | | | | 5 | 11 | 10 | 11 | 37 | 5.29 | 11 |
| $F_1 \times F_1$ (3 × 3)[1] | 17 | 21 | 11 | 7 | 2 | | | 58 | 2.20 | 22 |
| 6 × 1[2] | 5 | 23 | 8 | 1 | 1 | | | 38 | 2.20 | 0 |

It can be seen from a glance at this table that the variation in amount of darkness is a continuous one, from a gray-bellied agouti dorsally all-black, through every possible gradation to a wild-type segregate. The continuous nature of the variation was noted throughout the grading of the dark agoutis in the ever-present tendency to create more classes for the young by adding half and even quarter grades, a temptation which was yielded to only in the grade 5.5, this grade being given to dark agoutis which showed many agouti hairs on shoulders and legs. There is nowhere any evidence of a simple unit-difference between wild agouti and the darkener derived from black-and-tan. The only segregation is that seen in grade 1 animals which bred true and gave no evidence of possessing the darkener.

The above statements are not intended to be final. To date the evidence indicates the presence of a continuously variable and non-Mendelian character which gives the appearance of a blend in cross-bred young, and which in the pure black-and-tan race has been added to yellows carrying black and has darkened and increased their black pigment to the greatest possible extent. The evidence has failed to exclude wholly the possibility of interpreting the darkness of black-and-tan by multiple factors, but the contінous nature of the variation in hybrid young would call for the postulation of such a large number of modifiers that this view could be neither proved nor disproved. The nature of the darkener is still to be determined, but its action on both agouti and non-agouti young seems to be to increase the total amount of black or brown pigment produced.

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[1] From the cross black-and-tan × wild.

[2] Highest grade dark agouti × wild.

The experiments with the red race do not admit of as definite conclusions as were reached concerning black-and-tan, because of the difficulties of grading for intensity. It is safe to say, however, that red is a race in which yellow has been greatly intensified by a process similar to, though distinct from, that which has produced the darkness of the black-and-tan.